A SPATIALLY-STRUCTURED THREE-SPECIES MODEL SYSTEM FOR BENTHIC COMMUNITY

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Abstract

Recently Donalson et al [3] gave a one-prey (mussel) and one-predator (sea star) model-system representing the spatially-structured dynamics of benthic community. We generalize this model in this paper and extend its scope to the dynamics of three species of benthic community namely: mussel, sea star and spiny lobster.

Keywords: Spatially-structured; Benthic species; Predator prey interactions

1. Introduction

In a recent study Donalson et al [3] introduce four models (each model representing a different model class namely: ODE, SBD, CA and ABM; see [3] for details) of an intertidal predator-prey system to demonstrate advantages of the multiple model approach. They introduce an experimental system of mussels and their predators. The mussel Mytilus californianus is a dominant species of the intertidal zones of the North American continent. This species is found in narrow bands in shore sites of moderate to high wave exposure. The predators of M. californianus are the sea star, Pisaster ochraceus, in the Pacific Northwest [6, 7], and the spiny lobster, Panulirus interruptus, in Southern California [8].

Early experiments suggested that mussels experience a spatial refuge from predation at the upper intertidal zone. Paine [6] observed that below the upper intertidal zone there were patches of very large mussels which escape predation. It had also been observed that sea stars ate mussels smaller than the maximum available size. This suggested that mussels reach a certain size and become resistant to predation. Later studies contradict the hypotheses of spatial and size refuges [4, 9] terming the refuge hypothesis as an oversimplification of a more complex situation. Mussel growth depends on the flow of water providing food, resulting in higher growth rates for mussels located in the intertidal

zone and on wave exposed shores [2]. The probability of being attacked by a predator decreases when a mussel is surrounded by larger mussels [9, 10]. Thus, the rates of production and mortality in any specific location depend on the location of a mussel in the gradients of tidal height and wave exposure and on the size and density of surrounding mussels. Authors in [3] incorporate these assumptions in their models considering rates of recruitment, growth, and predation mortality as dynamic spatially explicit process.

As has been pointed out above, authors in [3] take a multiple model approach and develop and analyze four classes of models to study the predation dynamics in benthic communities. Their ODE model is a two-species model that represents the dynamics of a single prey (mussel) and its single predator (sea star or spiny lobster) in the Pacific. We generalize this model in this paper and extend its scope to represent the interactive dynamics of those regions of Pacific where all the three species i.e. prey (mussel) and its two predators (sea star and spiny lobster) interact.

It may be noted that although our three-species model has been designed keeping the dynamics of mussel and its predators in view, its results can still be applicable to other similar situations of fish interactions.

2. The Model

Our model is based on the work of Donalson et al [3] where "space" is made up of a large number of very small "patches" which can be occupied by at most one mussel and predators move randomly among patches. Prey biomass grows in size in each patch until a predator grazes a patch to size zero. In our model, each patch is either empty or occupied by a mussel. We give the model as a system of three differential equations:

$$\frac{\partial n(a,t)}{\partial t}+\frac{\partial n(a,t)}{\partial a}=-\mu(a,t)n(a,t), \tag{1}$$

$$\frac{dP(t)}{dt}=I_1-\alpha_1(t)P(t), \tag{2}$$

$$\frac{dQ(t)}{dt}=I_2-\alpha_2(t)Q(t), \tag{3}$$

where $n(a,t)$ is the density of prey of age a at time t; $P(t)$ and $Q(t)$ represent the densities of two types of predators. Equation (1) is the well known Mckendrick model [5] for removals in an age-structured population with $\mu(a,t)$ denoting the mortality rate for prey of age a at time t.

We assume that the addition of new individuals into prey population takes place according to $n(0,t) = \sigma(1 - N(t)/K)$ where σ is the constant rate at which the preys settle into empty patches with overall recruitment of prey decreasing linearly until all available space is occupied at a maximum density K. $N(t)$ represents the overall prey density to be given by $N(t) = \int_0^\infty n(a,t)da$. In the above open system, predators $P(t)$ and $Q(t)$ immigrate at the constant rates I_1 and I_2 and emigrate at the per capita rates $\alpha_1(t)$ and $\alpha_2(t)$ respectively.

Considering that the prey (mussel) size plays an important role in its protection from predation, we let $s(a)$ denote the size of a prey of age a and assume growth to be given by the von Bertalanffy [1] formulation $s(a) = s_\infty - (s_\infty - s_0)\exp(-\beta a)$, where β is the growth rate, s_∞ is the maximum size, and s_0 is the size of a newly settled recruit. We assume each prey's vulnerability to predation depends on its size and density and size of prey in some spatial neighbourhood of radius R surrounding the individual. Following authors of [3] in their mean field approximation, we consider the size of the neighbourhood $R = \infty$, and define $S(t) = \int_0^\infty s(a)n(a,t)da$ as the mean size of prey weighted by prey density. We write the mean field approximation for the per capita mortality rate of prey as:

$$\mu(a,t) = \mu_0 + [\theta_1(t)P(t) + \theta_2(t)Q(t)]\exp(-cS(t)), \quad (4)$$

which is independent of prey age but decreases exponentially with the weighted mean size of prey, $S(t)$. The parameter μ_0 is the mortality rate due to causes other than predation, θ_1 and θ_2 are the respective predatory rates of predators $P(t)$ and $Q(t)$, and c is a measure of how quickly resistance to predation increases with prey size. We assume that the prey defends more against a predator species that is more abundant compared with the population of the other predator species. We incorporate this assumption in its simplest form by considering the following forms for the predatory rates θ_1 and θ_2:

$$\theta_1(t) = k_1(1 + P(t)/Q(t))^{-1} \text{ and } \theta_2(t) = k_2(1 + Q(t)/P(t))^{-1} \quad (5)$$

Here k_1 and k_2 are the predation coefficients of predators $P(t)$ and $Q(t)$ respectively. It may be noted that the predatory rates θ_1 and θ_2 are a special case of a more general prey defensive switching functions given in [11]. Interested reader may consult [11] for more details on defensive switching. For predators, we assume that the emigration rate of each predator from the system is inversely proportional to the per capita rate of prey consumption. We consider

$$\alpha_1(t) = \frac{E_1(P+Q)}{[k_1 QS(t)\exp(-cS(t))]} \quad \text{and} \quad \alpha_2(t) = \frac{E_2(P+Q)}{[k_2 PS(t)\exp(-cS(t))]}, \tag{6}$$

where E_1 and E_2 are the constants of proportionality relating prey consumption to predator emigration. Taking the time derivative of $S(t)$ and using the expression for $n(0, t)$ and the equations (4)-(6), one can replace the Mckendrick equation (1) with a pair of ordinary differential equations and thus model equations (1)-(3) can be written as:

$$\frac{dS}{dt} = s_0\sigma + (s_\infty\beta - s_0\sigma K^{-1})N(t) - (\beta + \mu_0 + \frac{(k_1+k_2)P(t)Q(t)\exp(-cS(t))}{P(t)+Q(t)})S(t)$$

$$\frac{dN}{dt} = \sigma - (K^{-1}\sigma + \mu_0 + \frac{(k_1+k_2)P(t)Q(t)\exp(-cS(t))}{P(t)+Q(t)})N(t)$$

$$\frac{dP}{dt} = I_1 - \frac{E_1(P(t)+Q(t))P(t)}{k_1 Q(t)S(t)\exp(-cS(t))},$$

$$\frac{dQ}{dt} = I_2 - \frac{E_2(P(t)+Q(t))Q(t)}{k_2 P(t)S(t)\exp(-cS(t))}. \tag{7}$$

It may be noted that this system of equations is a modified version of the "patch approximation model" or PAM of [3].

3. Equilibrium Solutions

Setting $dP/dt = dQ/dt = dN/dt = 0$, one can solve for the equilibria P_1, Q_1 and N_1 in terms of S. Substituting these expressions into the equation for $dS/dt = 0$, model equilibria can be obtained as positive real roots of the function:

$$f(S) = s_0\sigma[K^{-1}\sigma + \mu_0 + \frac{(k_1+k_2)ABS\exp(-2cS)}{(1+A)^2}] + [\beta s_\infty - K^{-1}s_0\sigma]\sigma -$$

$$s[\beta + \mu_0 + \frac{(k_1+k_2)ABS\exp(-cS)}{(1+A)^2}][K^{-1}\sigma + \mu_0 + \frac{(k_1+k_2)ABS\exp(-2cS)}{(1+A)^2}] = 0, \tag{8}$$

where $A = \sqrt{I_1 k_1 E_2 / I_2 k_2 E_1}$ and $B = \sqrt{I_1 I_2 k_1 k_2 / E_1 E_2}$.

For the prey (N) and a single predator (say (P) we use the same data as given in [3] and reproduced here in Table 1. For the predator Q, we consider parameter values as shown in Table 2.

Table 1: *Model parameters and their default values from [3]**

Symbol	Definition	Value
area	Unit area	25 cm^2
A_r	Total system area	$4x10^4$ units of area
t	Time	1 day
a	Age	1 day
σ	Prey recruitment rate	1 prey (unit area)$^{-1}$ day^{-1}
s_0	Size of newly settled prey	1 mm

**Table 1 continued on the next page*

Table2: *Model parameters for predator Q with same units as given in Table 1.*

s_∞	Maximum prey size	200mm
β	Decrease in prey growth rate with size	.0004 day^{-1}
μ_0	Background per capita prey mortality rate	.0001 day^{-1}
K	Maximum prey density	1 prey (unit area)$^{-1}$
k_1	Attack coefficient of predator P	1.0 unit area Predator^{-1} day^{-1}
c	Resistance to predation with prey size	.04 unit area mm^{-1}
I_1	Immigration rate of predator P	.01 predator (unit area)$^{-1}$ day^{-1}
E_1	Emigration coefficient of Predator P	5.0 mm predator^{-1} day^{-2}

Sym-bol	**Defini-tion**	**Various values**
k_2	Attack Coeff.	0.1,0.7, 1.0,5.0, 20,30
I_2	Immigra-tion rate	.006,.01, 1.0, 50.0
E_2	Emigra-tion rate	2.0,5.0, 10.0

We observe from numerical calculations that if parameter values from Table 1 are taken along with any combination of values of parameters k_2, I_2, *and* E_2 including those from Table 2, then our model-system (7) has the possibility of multiple equilibrium solutions depending on the number of real positive roots of equation (8). More specifically, model-system (7) has either single equilibrium or three equilibriums. As an illustration, we show in Fig. 1 below the change in the roots of equation (8) over a range of values of the predation coefficient k_2 fixing $I_2 = 0.01, E_2 = 5.0$ (same as for predator P) and considering values of all other parameters according to Table 1.

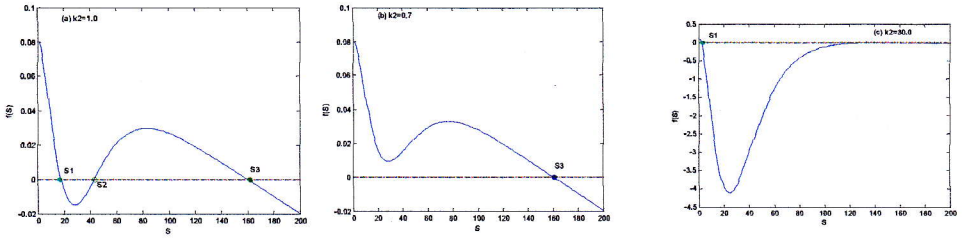


Fig. 1: *Roots of eqn. (8) over a range of values of predation coefficient* k_2. *(a) Three roots S1, S2 & S3 exist for* $k_2 = 1.0$ *(b) only upper root S3 exists for* $k_2 = 0.7$ *(c) only lower root S1 exists for* $k_2 = 30$.

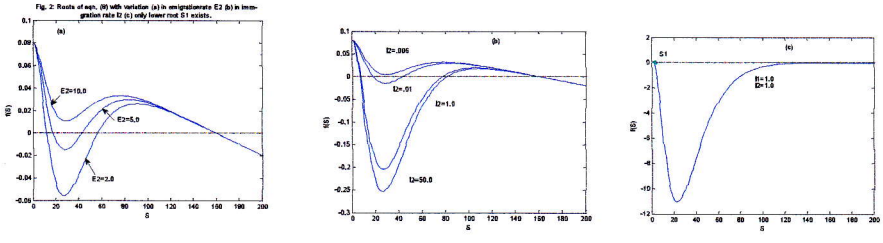
4. Stability of Equilibria

It can be seen using the default values of Table 1 and any suitable choice of values for parameters k_2, I_2, *and* E_2 and integrating the model-system (7) by MATLAB ODE solvers ode45 or ode23s that the lower equilibrium $e_1 = (S_1, N_1, P_1, Q_1)$ and the upper equilibrium $e_3 = (S_3, N_3, P_3, Q_3)$ of model-system (7) are stable where as the middle equilibrium $e_2 = (S_2, N_2, P_2, Q_2)$ is unstable. Here S_i is a positive real root of equation (8) and N_i, P_i, Q_i are the corresponding equilibrium values for prey N, predator P & predator Q.. At the lower stable equilibrium e_1, prey density and sizes are kept low by (relatively) high levels of total predation by both predators. At the upper stable equilibrium e_3, there is a relatively high density of large prey which are resistant to predation. The unstable equilibrium e_2, lies in-between the two stable equilibria. A solution of model-system (7) tends to which of the two stable equilibria depends on the initial point. For the default values of Table 1 and $I_2 = 0.01$, $E_2 = 5.0$ (same as for predator P), model-system (7) has only the upper stable equilibrium e_3 if the predator attack rate $k_2 < 1$, has three equilibria if $1 \le k_2 \le 25$ and only the lower stable equilibrium if $k_2 \ge 30$. Under the similarity conditions for both predators as mentioned above when the two predators differ only in their attack rates, it is seen that the predator whose attack rate is higher maintains its higher density at either stable equilibrium. But if the two predator populations are identical then at either stable equilibrium both predators maintain equal densities. These observations are based on the values of equilibria given in Table 3 below:

Table 3. *Equilibria of model system (7) for default parameter values of Table 1 and* $I_2 = 0.01$ *and* $E_2 = 5.0$.

k_2	**Lower stable equilibrium** $e_1 = (S_1, N_1, P_1, Q_1)$	**Upper stable equilibrium** $e_3 = (S_3, N_3, P_3, Q_3)$
0.1	----------	(160.1663, 0.9999, 0.00012, 0.00004)
0.7	----------	(160.0854, 0.9999, 0.00024, 0.00020)
1.0	(17.4292, 0.9956, 0.0087, 0.0087)	(160.0439, 0.9999, 0.00026, 0.00026)
5.0	(4.9625, 0.9811, 0.0056, 0.0126)	(159.3422, 0.9999, 0.00037, 0.00084)
20.0	(2.3283, 0.9485, 0.0035, 0.0155)	(154.4633, 0.9999, 0.00052, 0.00230)
30.0	(1.9341, 0.9315, 0.0030, 0.0166)	----------

In the following Fig. 2, we show the roots of equation (8) and hence the equilibia of model-system (7) for the default parameter values of Table 1 but when the predator Q differs with predator P in the emigration and immigration rates. In Fig. 2(a) $k_2 = 1.0, I_2 = 0.01$ (b) $k_2 = 1.0$, $E_2 = 5.0$ and (c) $k_2 = 1.0$, $E_2 = 5.0$, $I_1 = 1.0$, $I_2 = 1.0$.



It is evident that the lower emigration rates give two stable equilibria but for higher emigration rates only upper stable equilibrium exists. Contrary to this, large immigration rates provide two stable equilibria whereas for lower immigration rates only upper stable equilibrium exists. Interestingly if the immigration rates of both predators are equal to or greater than 1 then only lower stable equilibrium exists as shown in Fig. 2(c).

For chosen feasible parameter values as those in Tables 1and 2, there is no evidence of exotic dynamics such as limit cycles or chaos.

5. Harvesting

As pointed out in the introduction our three species model-system (7) can be applicable to those situations of fish interactions which have vital parameters similar to mussel and their predators. To introduce periodic harvesting of prey in the model-system (7), we modify equation (7b) and rewrite it as model-system (9) given below

$$\frac{dS}{dt} = s_0\sigma + (s_\infty\beta - s_0\sigma K^{-1})N(t) - (\beta + \mu_0 + \frac{(k_1 + k_2)P(t)Q(t)\exp(-cS(t))}{P(t)+Q(t)})S(t),$$

$$\frac{dN}{dt} = \sigma - (K^{-1}\sigma + \mu_0 + \frac{(k_1 + k_2)P(t)Q(t)\exp(-cS(t))}{P(t)+Q(t)})N(t) - h(1+\sin(\omega t)),$$

$$\frac{dP}{dt} = I_1 - \frac{E_1(P(t)+Q(t))P(t)}{k_1Q(t)S(t)\exp(-cS(t))},$$

$$\frac{dQ}{dt} = I_2 - \frac{E_2(P(t)+Q(t))Q(t)}{k_2P(t)S(t)\exp(-cS(t))}. \quad (9)$$

Here h is the rate of harvesting and ω is related to period of harvesting. As an example we consider the default parameter values of Table 1 and assume that the predator Q also has its vital parameters similar to predator P such as $I_2 = 0.01$ and $E_2 = 5.0$ but differs only in its predation coefficient with $k_2 = 5.0$. Note that all the parameter values have been chosen from Tables 1 and 2. We assume, $h = 0.1$ $\omega = 0.5$ and integrate model-system (9) using MATLAB ODE solver ode 23s from $t = 0$ to $t = 5000$ with initial point at $(110.0, 2.0, 1.0, 1.0)$. It is seen that periodic harvesting may lead to coexistence of all the three species in an oscillatory manner as is shown in the following Fig. 3.

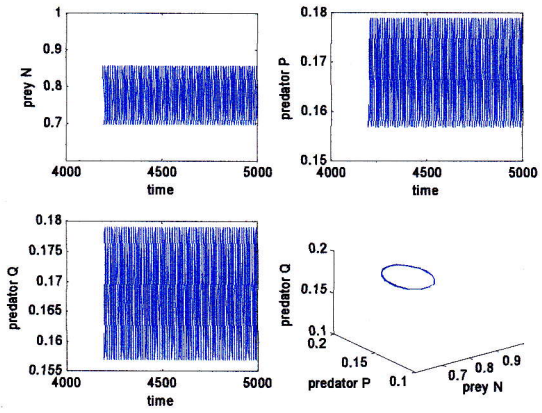


Fig. 3: *Coexistence of three species in an oscillatory manner due to periodic harvesting.*

Conclusions

We give in this paper a three-species model that represents the predation dynamics of spatially-structured species of benthic community namely: mussel, sea star and spiny lobster. It is seen that the model has the possibility of multiple stable equilibria. Using the default parameter values for the prey and one of the predators from Table 1 and considering various values of the parameters for the other predator, it is found that (i) the prey density and sizes are kept low by relatively high levels of total predation at the lower stable equilibrium (ii) there is a relatively high density of large prey resistant to predation at the upper stable equilibrium (iii) when the predators differ only in their attack rates then the predator whose attack rate is higher maintains it higher density at either stable equilibrium (iv) lower emigration rates give rise to two stable equilibria but contrary to this, large immigration rates provide two stable equlibria. Finally, it is seen that if the prey population is harvested periodically then all the three species coexist in an oscillatory manner.

References

1. L. von Bertalanffy, "A Quantitative Theory of Organic Growth", *Human Biology* **10** (1938), 181-213
2. E.F. Dahlhoff & B.A. Menge, "Influence of Phytoplankton Concentration and Wave Exposure on the Ecophysiology of Mytilus Californianus", *Marine Ecol. Progress Series* **144** (1996), 97-107.
3. D.D. Donalson, R.A. Desharnais, C.D. Robles & R. Nisbet, 'Spatial Dynamics of a Benthic Community: Applying Multiple Models to a Single System*" in Scales in Aquatic Ecology: Measurement, Analysis and Simulation*, (eds.) P. Strutton & L. Seuront, (CRC Press, 2003).
4. B.F.J. Manly, "Comments on Design and Analysis of Multiple-choice Feeding-preference Experiments", *Oecologia* **93** (1993), 149-152.
5. A.G. McKendrick, "Applications of Mathematics to Medical Problems", *Proc. Edinburg Math. Soc.* **44** (1926), 98-130.
6. R.T. Paine, "Intertidal Community Structure: Experimental Studies on the Relationship between a Dominant Competitor and its Principal Predator", *Oecologia* **15** (1974), 93-120.
7. R.T. Paine, "Size Limited Predation: An Observational and Experimental Approach with the Mytilus Pisaster Interaction", *Ecology* **57** (1976), 858-873.
8. C.D. Robles & J. Robb, "Varied Carnivore Effects and the Prevalence of Intertidal Algal Turfs", *Journal of Exp. Marine Biology and Ecology* **166** (1993), 65-91.
9. C. Robles, D.A. Sweetnam & J. Eminike, "Lobster Predation on Mussels: Shore-level Differences in Prey Vulnerability and Predator Preference", *Ecology* **71** (1990), 1564-1577.

10 C. Robles, R. Sherwood-Stephens & M. Alvarado, "Responses of a Key Intertidal Predator to Varying Recruitment of its Prey", *Ecology* **76** (1995), 565-579.

11 M. Saleem, A.K. Tripathi and A.H. Sadiyal, "Coexistence of Species in a Defensive Switching Model", *Math. Biosciences* **181** (2003), 145-164